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SURFACE ADAPTATIONS OF THE VERTEBRATE EPIDERMIS TO FRICTION

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Epidermal surfaces in representative vertebrates specialized for lowered or increased friction were studied with the scanning electron microscope. Microvillous and microridged patterns predominate in aquatic vertebrates. In squamate reptiles, the complex and varied ornamentation of the Oberhäutchen functions both in adhesive modifications and in modulating surface reflectivity. Frictional surfaces in birds and mammals are characterized more by anatomical than by cytologic specializations, the detailing of surface cells being mostly a function of turnover rate.

The vertebrate epidermis is exposed to various, often conflicting, demands in its interaction with the environment. A smooth slimy surface, for example, has hydrodynamic advantages but would prove a locomotory hazard in an amphibious mode of life. An arboreal habitat puts a higher premium on a tenacious grip than does a slow plodding along the ground. In addition to obvious anatomical adaptations, the epidermis supplements these varied frictional requirements in vertebrates by a wide spectrum of surface modifications, to whose study the scanning microscope is uniquely suited. A detailed ultrastructural survey of the sectioned vertebrate epidermis has been published by Parakkal and Alexander [1] and serves as a valuable complementary reference to this article.

MATERIALS AND METHODS

Skin from the species studied was pinned out, fixed, and dehydrated in that condition. Single fixation was usually sufficient and consisted of phosphate- or s-collidine-buffered solutions with 1% glutaraldehyde, 4% formalin, and 1% acrolein or a modified fixative for amphibian embryos [2,3]. The tissue was critical-point dried in Freon, gold-palladium coated in a sputtering device (Technics, Inc.), and viewed in an AMR 1000 scanning electron microscope at 10 kv.

Species examined included:

Entosphenus tridentatus (Pacific lamprey, larval and adult)
Salmo gairdneri (Steelhead trout)
Taricha torosa (California newt, larval)
Bufo alvarius (Colorado River toad)
Rana pipiens (Leopard frog)
R. catesbeiana (Bullfrog)
Anolis carolinensis (American chameleon)
Thamnophis elegans (Western garter snake)
Gallus domesticus (Chick)
Cavia porcellus (Guinea pig)
Rattus rattus (Rat)
Bos taurus (Cow)
Homo sapiens (Man)

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OBSERVATIONS AND DISCUSSION

To lower frictional drag in water, aquatic lower vertebrates rely largely on a mucous coating of the epidermis. Hence, their surfaces are usually microvillous (Fig. 1) and probably function more to anchor mucus than in any direct hydrodynamic interaction; the latter function has been suggested for the protruding placoid scales of sharks. The lamprey larva burrows in sandy river bottoms, where mucous secretion is especially important [4]. Trout epidermal cells are covered with a complex, whorled, or reticulated array of microridges [3] (Fig. 2), visually a striking deviation from a microvillous pattern, but probably functionally similar. Boundaries between cells are commonly outlined by facing low ridges or rows of microvilli, whose conspicuous nature may be associated with the mechanical stresses on the subjacent junctional complex.

The epidermis of the larval salamander corresponds to the preceding examples by being covered with microvilli or microridges [5] and the addition of occasional ciliated cells (Fig. 3). Marked concentration of cilia over the external gills and around the nares implies that the cilia function in respiration and olfaction by moving water or fluid mucus over the surface of the epidermis. The superficial mucous layer is presumably less cohesive than that of fishes. The adoption of saltatory locomotion or an arboreal habitat by frogs clearly demands a more secure frictional surface than the unmodified mucous body surface provides. At the periphery of frog toe pads, the shallow relief of the epidermis becomes acutely accentuated by raised cells and depressed zones of abutment, which in some species contain a conspicuous raised ridge over the line of cellular contact [6,7] (Fig. 4). The cells have unusually broad, flat-topped microvilli with a network of depressions corresponding to the im-

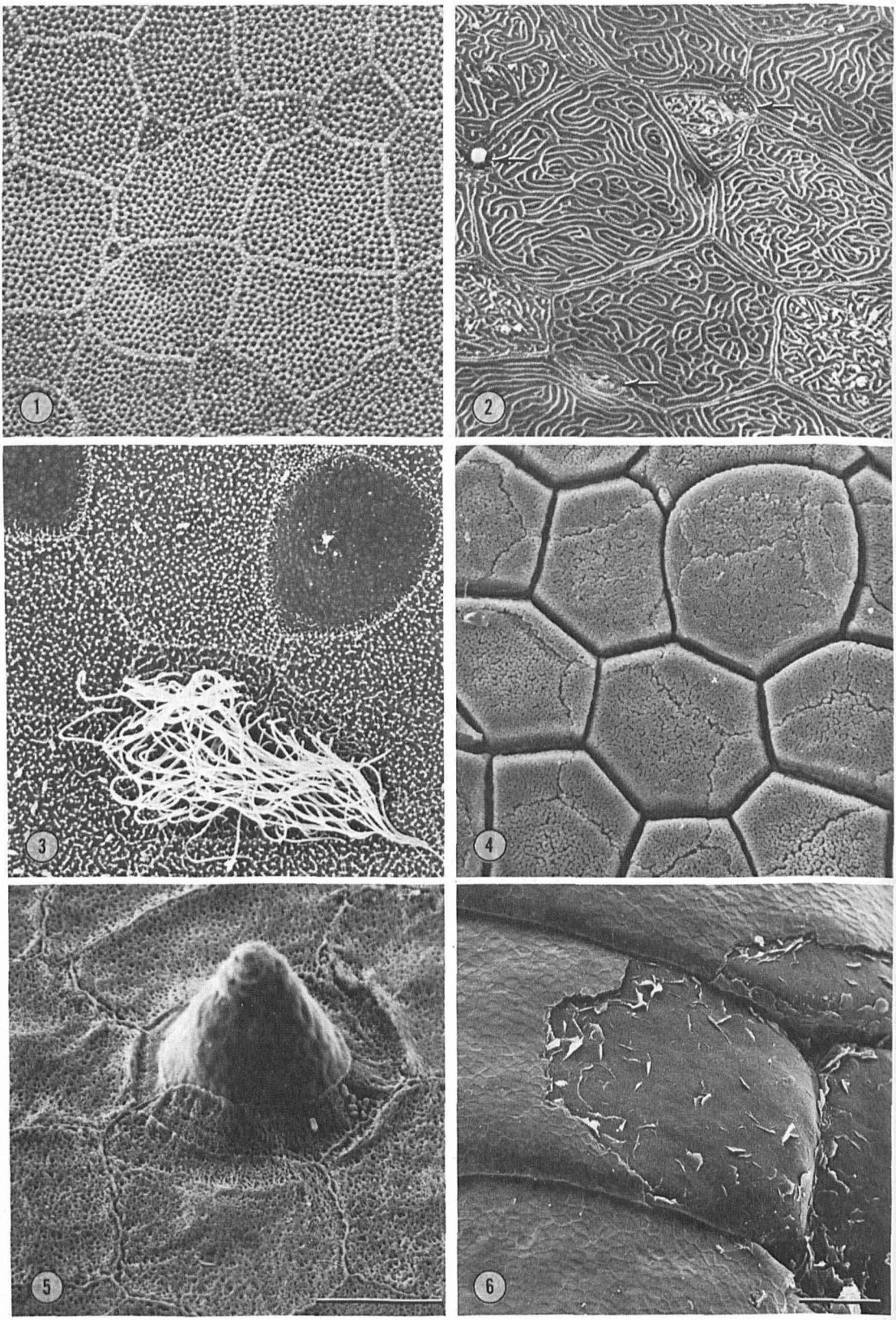


FIG. 1. Epidermal surface of lamprey larva (*Entosphenus tridentatus*). Stubby microvilli outline boundaries of adjacent cells (× 2,000).

FIG. 2. Microridges on trout epidermis (*Salmo gairdneri*). Unicellular mucous glands are scattered between

print of the previous overlying epidermal generation. In some tree frogs, the epidermal cells of the toe pads are set with long, brushlike microvilli [6].

The epidermal cells of the one toad studied are rather uniform, with a reticulated surface pattern and small marginal ridges. The surface is studded with unicellular tubercles, 10 to 20 μ high, whose smooth surface structure suggests that they are more fully cornified than is common in unspecialized amphibian epidermis (Fig. 5). Although the toad epidermis contains an abundance of unicellular glands, its surface is presumably more protected by the projecting tubercles than by any secreted coating. In keeping with the slow lumbering gait of the toad, its toe pads have no unusual modifications.

Purely epidermal specializations reach their zenith in reptiles, specifically snakes and lizards [8–12]. The epidermis of these animals is composed of several distinct layers which are generated and shed discontinuously. The outermost of these is the Oberhäutchen, a thin compact layer of β-keratin, whose cellular outlines are completely obliterated. The surface decoration of the lizard Oberhäutchen runs the gamut from smooth, pitted, microridged, lamellate, dentate, to spinulate [13,14] (Fig. 7). In most cases, these textures appear to be related to a modulation of surface reflectivity, but several remarkable instances of frictional adaptations are known. The gecko *Teratoscincus* makes cricket-like sounds by lashing its tail, during which overlapping dorsal scales rub across the spinulate Oberhäutchen of adjacent ones [15], one of the rare examples of nonrespiratory sound production in vertebrates.

The most elaborate specialization of the Oberhäutchen is seen in the foot pads of gekkonid and anolid lizards [16–19]. The lower surface of the toes is subdivided into 10 to 25 transverse or chevron-shaped lamellae (Fig. 8). In *Anolis*, these are set with up to 20 μm-long setae, actually large spinules of the Oberhäutchen. Each one is expanded at the tip into a small pad about 1 μm wide (Fig. 9). With an estimated 150,000 to 200,000 setae per toe, geckos can climb up vertical glass surfaces and cling securely to ceilings. This adhe-

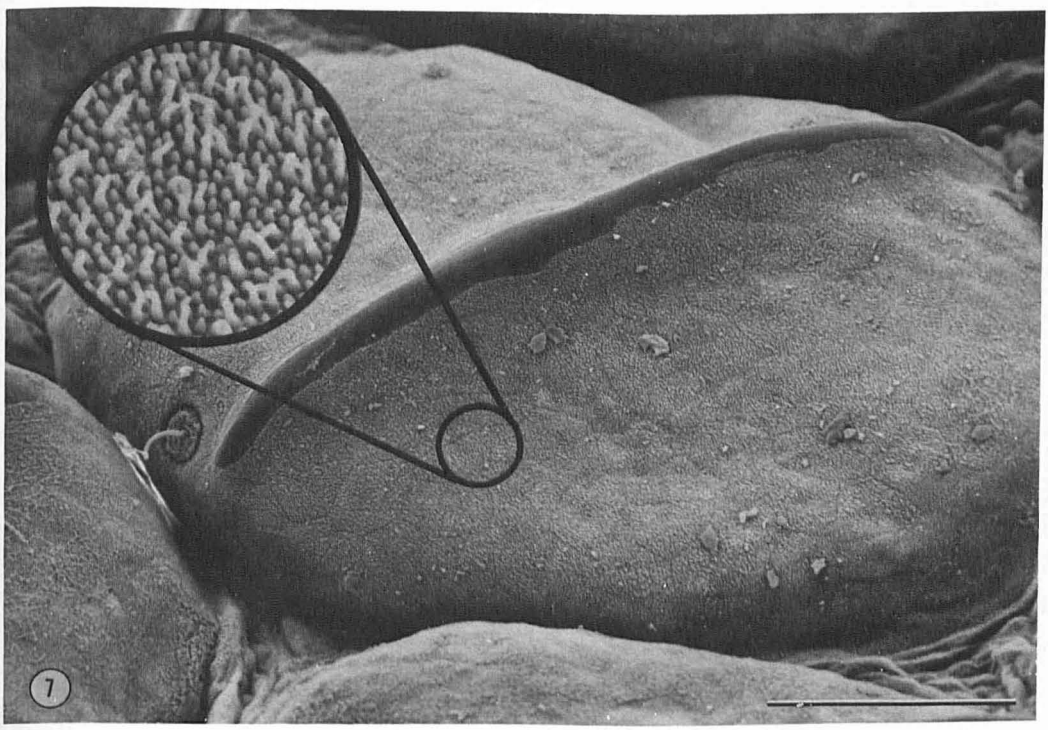


FIG. 7. Dorsal scale of the American chameleon (*Anolis carolinensis*). The spinulate Oberhäutchen shows the faint imprint of the clear layer, the overlying stratum of the preceding epidermal generation. The small annular structure at the rear of the scale (left) is a presumptive tactile sense organ (× 640; *inset* × 6,000). Bar equals 50 μm.

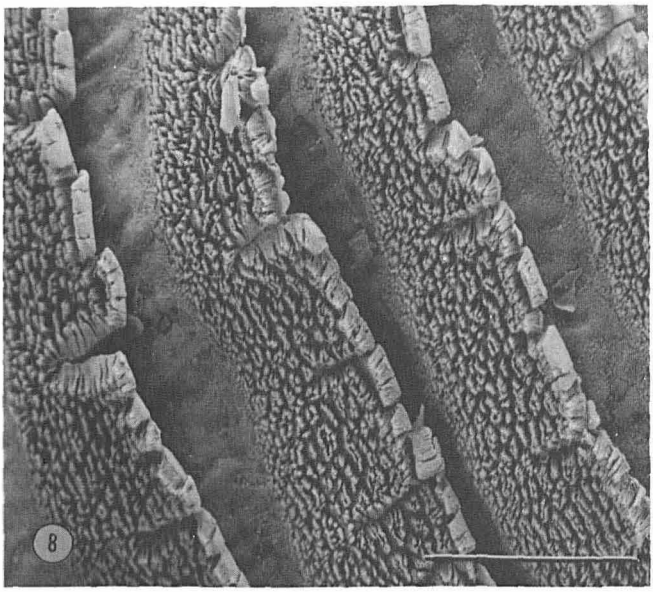
epidermal cells (*arrows*) (× 2,000).

FIG. 3. Ciliated and microvillous cells from the head of a salamander larva (*Taricha torosa*). The significance of the smooth cells is unknown (× 2,000).

FIG. 4. High-relief cells from a frog's toe pad (*Rana pipiens*). The squat microvilli show the indentations of the previous epidermal generation (× 2,000).

FIG. 5. Epidermal tubercle and surrounding reticulated cells from the back of a toad (*Bufo alvarius*) (× 2,000). Bar equals 10 μm.

FIG. 6. Scales on the leg of a 1-day-old chick. The embryonic periderm (left) is sloughing off and revealing the underlying, rather smooth epidermis of the adult (× 130). Bar equals 100 μm.



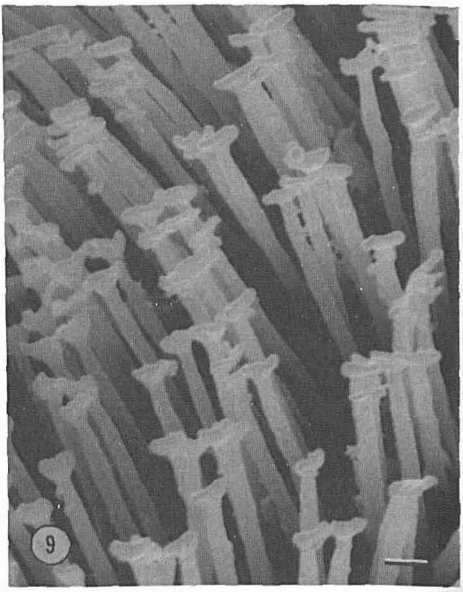
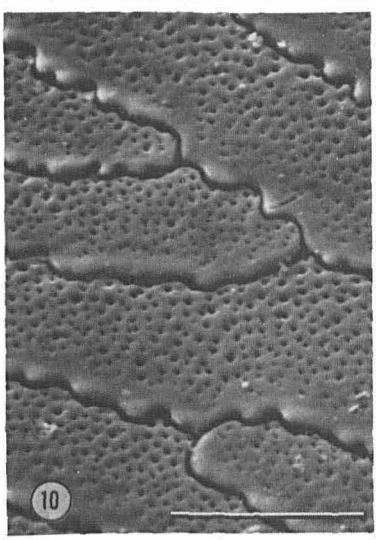
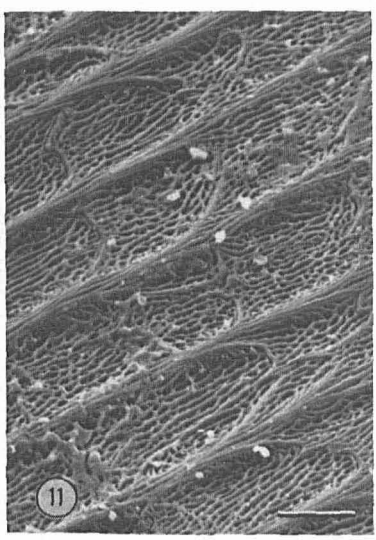
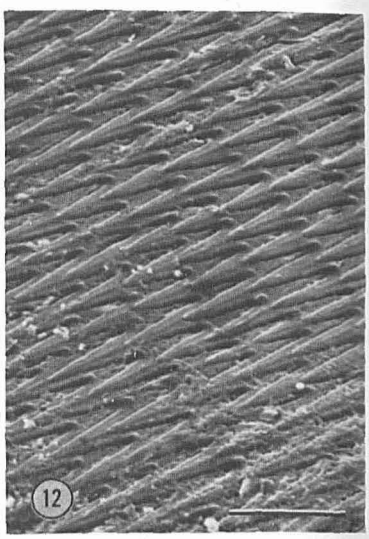


FIG. 8. Digital lamellae of *Anolis carolinensis*. The tip of the toe is toward the upper right. The long setae grade into normal spinules in the basal zone of the lamellae, both being part of the Oberhäutchen (× 270). Bar equals 100 μm.
FIG. 9. Digital adhesive setae of *Anolis carolinensis* with expanded, pad-like tips (× 5,500). Bar equals 1 μm.







FIGS. 10–12. Decorations of the Oberhäutchen on the head, back, and belly of a snake (*Thamnophis elegans*), respectively, illustrating the lamellate, reticulate, and dentate condition (Fig. 10: × 5,000; Fig. 11: × 2,000; Fig. 12: × 3,000). Bar equals 5 μm.

sion to the substratum is apparently made possible by a large percentage of the several million flexible setae that contact the substratum, a force which could not be generated by the contact of two smooth surfaces of equal area because of the inevitable few, scattered points of contact.

Differences in the ornamentation of the snake Oberhäutchen may be species specific [20]. Several such distinct patterns, however, are seen on different regions of the garter snake body (Figs. 10–12). The scales on the head have a finely pitted, shingled surface, whereas those on the body are longitudinally ridged and surfaced with smooth or reticulated spinules or denticles tightly appressed to the surface. In all of these patterns, the underlying distribution of cells has been totally effaced during keratinization, the ornamentation maintaining unbroken continuity across entire scales. All of these surfaces appear to be entirely adapted to lowered friction.

The transition from an aquatic to a terrestrial environment is strikingly illustrated in the skin of a newly hatched bird, in which the embryonic periderm, to all intents appearing like microvillous amphibian epidermis, is shed to reveal the underlying adult, desquamating epidermis [21,22] (Fig.

6). Frictional regions, such as beak and feet, have a rather tightly structured surface of smooth squames, but over the rest of the body the intricate architecture of feathers controls aerodynamic friction.

Unlike the diverse surface architecture of the preceding examples, mammalian epidermal cells [23,24] have a rather limited decorative scope, ranging from the deeply reticulated surface cells of the cow snout, a moist and heavily abraded epidermis (Fig. 14), through the microvillous or ridged epidermal surfaces found in various abnormal skin conditions or within the epidermis [25–27], to the exposed, desquamating surface with minimal surface detailing. These differences are due partly to the average state of moistness of the pertinent epidermis, which is provided by the surface cover of sweat or mucus, the rate of epidermal proliferation, and, hence, the time period of cellular drying. That genetic factors are also involved is seen in the extremely smooth-surfaced spines of the rat glans penis (Fig. 13), which are surrounded by rather heavily textured mucosal cells, both types existing in the identical environment. On such constantly dry, frictionally stressed surfaces as claws, hoofs, or nails, the surface relief is defined more by the degree of abrasion than by the structure of individual cells. Other regions of frictional loading, such as the friction ridges on the toes and fingertips of primates (Fig. 15), are characterized by an absence of built-up epidermal cells, a conspicuous feature of nonabraded skin (Fig. 16). Evenly spaced and crucially located sweat gland openings have a bearing on frictional properties, but no apparent

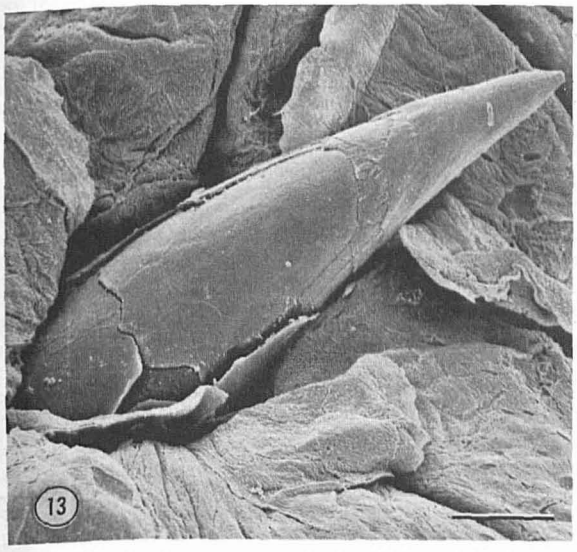
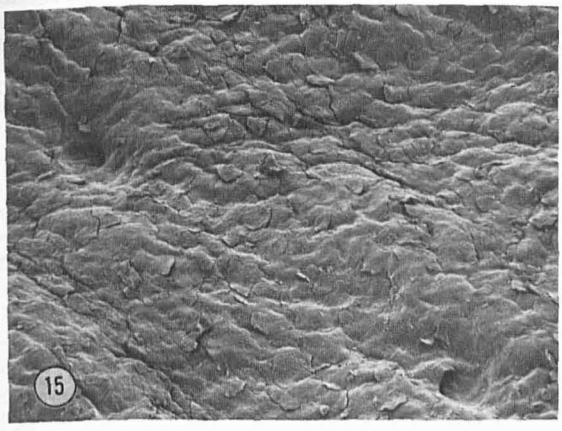


FIG. 13. Epidermal spine on the rat glans penis. Surrounding cells are reticulated, though the spin has a smooth surface (× 1,300). Bar equals 10 μm.

FIG. 14. Surface of the cow snout. At the right margin, a turned-back cell shows a microvillous underside, presumably matching the deep reticulations of the lower cell (× 1,800). Bar equals 10 μm.



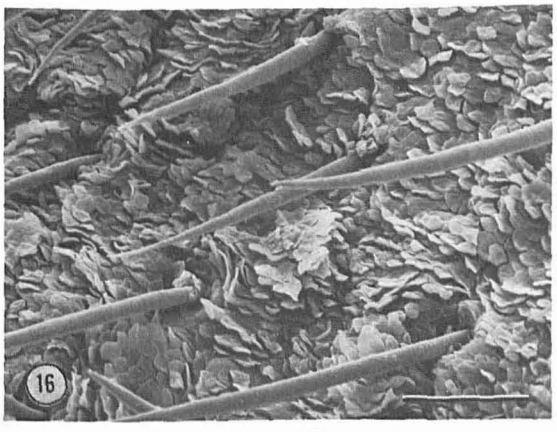


FIG. 15. Friction ridge from the thenar palm of a human female. Sweat ducts open along the top of the ridge, which has a minimum of loose squames (× 160).

FIG. 16. A low-friction surface with conspicuous accumulation of squames (tip of guinea-pig ear) (× 160). Bar equals 100 μ.

effect on the surface pattern of adjacent epidermal cells.

Hair plays not only a thermal and decorative role but, with respect to friction, a protective one as well. This is suggested by the diversity of hair sizes in any one animal alone, not to mention the range of diameter from 0.4 μm at the tip of a mole hair to 3 mm for a porcupine quill. Cuticle patterns, though exotic in the very thin hairs of some species, are relatively uniform in hairs with large diameters, differing mainly in the degree of tightness of adhesion. Continuous abrasion denudes the hair of cuticle and makes the exposed medullary core subject to fraying and longitudinal splitting.

The principal generalizations to be drawn from these observations are (1) that in some instances epidermal surface modifications are related to reflectivity, i.e., heat absorption, rather than to friction, and (2) that lower vertebrates excel in cellular specializations for frictional purposes, whereas faced with a conspicuous uniformity of epidermal cells, higher vertebrates, particularly mammals, have evolved anatomical adaptations instead.

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